A TAXONOMIC REVISION OF PODOCARPUS, XIII SECTION POLYPODIOPSIS IN THE SOUTH PACIFIC

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SECTION POLYPODIOPSIS was established in 1874 by Bertrand (1) for *Podocarpus vitiensis* Seemann, then known only from Fiji. In 1903, Pilger (23) included this species and *P. minor* Parlatore as species of doubtful affinity in sect. NAGEIA, chiefly because of their opposite leaves. In 1926, he mentioned Bertrand's section and species synonyms briefly but did not change his interpretation. Florin (8) recognized the significant differences of these species from others in sect. NAGEIA and restored the use of sect. POLYPODIOPSIS, to which he added *Podocarpus rospigliosii* Pilger, a South American species which had been described by then. This section now is firmly established in its use by Orr (22), Wasscher (32), and Buchholz & Gray (4).

The five living species now included in sect. POLYPODIOPSIS are *Podocarpus vitiensis* Seemann, of Fiji, New Guinea, New Ireland, and the Solomon Islands; *P. filicifolius* sp. nov., newly described from the Moluccas; *P. comptonii* Buchholz and *P. minor* Parlatore, endemic to New Caledonia; and *P. rospigliosii* Pilger, of the Andes of Venezuela, Colombia, and Peru. Two fossil species (from Tertiary deposits) referred to this section are *P. araucoensis* (Berry) Florin, found in Chile, and *P. brownei* Selling, lately described from Tasmania.

This distribution is striking and becomes very significant in recent studies of regional floras (Smith 28), monographs (e.g., Van Steenis 30, Selling 26), conifer geography (e.g., Florin 9, Li 20), and phylogeny (Florin 14). An ancient vast southern continental land mass is emphasized by Van Steenis (30) in his consideration of the angiosperm genus *Nothofagus*, which is not only found both in the South Pacific and South America, but which has a subsection of twenty-one species limited to New Caledonia and New Guinea. Some of the land areas here included are southeastern Asia, Australia, New Guinea, New Caledonia, Fiji, and New Zealand. Since *Podocarpus vitiensis* was known first from Fiji, the section has tended to be associated mainly with those islands, but with the discovery of the closely related *P. comptonii* in New Caledonia and of *P. filicifolius* in the Moluccas, the New Guinea area of *P. vitiensis* becomes

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of primary importance, with the Fijian specimens then representing an eastern extension of the species. There is a remarkably close similarity to the distribution of *Nothofagus* species. One would expect it to be possible to distinguish two separate species of *Podocarpus* from New Guinea and Fiji, but the specimens I have seen from New Guinea seem the same, and only ripe seeds are lacking from New Guinea. The close relationship of Fiji to these land areas, geologically and botanically, is shown especially well in the recent studies of the Fijian flora by Smith (28, 29).

The postulation of a great south land mass, often called Gondwanaland, would connect not only the continental islands of the South Pacific, but also Antarctica, Australia, Asia, South America and Africa.

The leaf anatomy of the species of sect. AFROCARPUS, endemic to Africa, shows the same twisting of the short petiole that is found in sect. POLYPODIOPSIS, even when the leaves are alternate instead of opposite. The species of both sections have amphistomatic leaves and the leaves lack accessory transfusion tissue; in the leaf epidermis of species of both sections, the subsidiary cells of the stomata show the Florin ring. The South American species, *Podocarpus rospigliosii*, is very like *P. vitiensis*, except that its branches are covered only with foliage leaves and we find scale leaves or bracts only on the fertile shoots; the seed usually is somewhat larger. Other gymnosperm genera with species in both South America and Australasia are *Araucaria*, *Dacrydium*, and *Austrocedrus*.

Florin (8, 11, 14) has concluded that *Podocarpus* is a southern genus which probably originated in the early Mesozoic, and we find fossil evidence in South America in *Podocarpus araucoensis* and in Tasmania in *P. brownei*. Florin's new fossil genus (11) from Australia belongs to sect. STACHYCARPUS of *Podocarpus* which has living species in South America, New Zealand, New Caledonia, and Australia. Buchholz (3) maintained the northern origin of all conifers.

The most significant change in recent gymnosperm systematics has been the separation of the taxads from the podocarps, leaving the latter with the conifers (Florin 10a,b, 12, 13, 14). Pilger (23), in his classical monograph of the Taxaceae, included the podocarps with the taxads. There was increasing indication that these should not be kept so close together, and, in 1926, Pilger arranged the gymnosperms in seven families with the Taxaceae and Podocarpaceae separated. This treatment was followed by Buchholz (2) in 1946, in spite of the growing realization that the taxads should not be included with other conifer families. Florin (14) compared these two groups morphologically in almost every way in which they could be investigated to uphold the elevation of a class Taxineae. This class has been based chiefly upon the evidence of the development of the female strobilus as found in fossils (Florin 10a,b, 13, 14). Wilde (33) limited her lengthy discussion to comparisons of the male and female strobili of many species of *Podocarpus*; she included many data, however, which were useful in deriving the interpretations and solutions given by Florin.

Only the two sections, POLYPODIOPSIS and NAGEIA, of *Podocarpus* regularly have opposite leaves; in sect. AFROCARPUS some specimens have all or only occasional branches with leaves opposite or subopposite. But all three of these sections show the peculiar twisting of the leaf bases and stem torsion In both sections POLYPODIOPSIS and NAGEIA, this may result in the leaves being spread in a single plane, as in the compound frond of a fern. This orientation has been described in detail by Florin (8), Orr (22), Gray & Buchholz (17), and Wasscher (32). Orr (22) recognized further similarities in sections POLYPODIOPSIS and AFROCARPUS in the leaf anatomy: the leaves are amphistomatic, with more or less hypoderm, transfusion tissue often extending more than half-way from the midrib to the margin of the leaf, no accessory transfusion tissue, and a single resin canal in all species except *P. rospigliosii*. The three resin canals below the vascular bundle, with additional ones in the blade of the leaf of *P. rospigliosii*, is an exception discussed by Gray & Buchholz (17) in relation to reports in the literature (e.g., Bertrand 1, Stiles 31, Mahlert 21) that *P. vitiensis* has more than a single vascular resin canal. The single resin canal which I have found in all transverse leaf sections of *P. vitiensis* is in agreement with the findings of Gibbs (16) and Orr (22) who emphasize this fact. Neither have I seen any accessory transfusion tissue in the mesophyll of the leaf blades such as is shown by Bertrand (1, *Pl. 6, fig. 12*). No mention has been made thus far that the notable difference in the leaves in sect. NAGEIA is in the many parallel veins extending the full length of the large leaf blades, in contrast to the single unbranched midrib of the species of sect. POLYPODIOPSIS.

Orr (22) used only three species in describing the leaf anatomy of sect. POLYPODIOPSIS: *Podocarpus vitiensis*, *P. rospigliosii*, and *P. minor*. The external appearance of the foliage of the two former is quite similar, and to these we may now add *P. filicifolius*, which has foliage most like that of *P. vitiensis*. The external appearance of *P. minor* differs in not showing the pinnate arrangement of the leaves in a single plane except in the foliage of seedlings and on occasional lower branches; the branches are otherwise fully covered with crowded, opposite, decussate, ascending, oval or elliptic leaves. The discovery in New Caledonia of *P. comptonii*, with transitional foliage, affirms the judgment that *P. minor* really belongs to this section. *Podocarpus comptonii* is a large tree, recognized by Compton (5) and others. It generally has the foliage which has been described in such detail, although the reproductive branches lose the pinnate arrangement and are covered with decussate, opposite, oval, or elliptic leaves, as seen in *P. minor*.

The only section of *Podocarpus* which has both bifacially flattened lanceolate leaves and scale leaves in the mature foliage is POLYPODIOPSIS. The two kinds of leaves in sect. DACRYCARPUS are scale leaves and the needle-like leaves on the pinnate twigs are tetragonal in transverse section. This remarkable dimorphism shown by the foliage on the main shoots and leafy branches was described by Florin (8) and Wasscher (32) for *Podocarpus vitiensis*, but it is also evident in the other species.

In his consideration of the external morphology of the coniferous leaves, De Laubenfels (6) described this section as having only Type II (bifacially flattened) leaves. The scale leaves (De Laubenfels Type III) have been found only in connection with mature foliage. This combination is rare among other gymnosperms, in fact, having been found only in seedlings of a *Dacrydium*; transitional foliage of *Chamaecyparis*, *Neocallitropsis*, and a *Dacrydium*; and mature foliage of *Athrotaxis*, *Taxodium*, and a group of *Juniperus*. *Podocarpus vitiensis* and *P. filicifolius* have scale leaves much as described by De Laubenfels, tapering sharply from the point of attachment and closely appressed to the stem in *P. vitiensis*. They are rarely crowded, except at the beginning of a growth period, but are usually spaced by internodes of about the same length as those between the foliage leaves. They are decurrent, and their arrangement is always decussate except at the one or two nodes immediately preceding distichous foliage leaves. *Podocarpus comptonii* and *P. minor* have some scale leaves of this kind but they become obtuse and ovate in shape, divaricate, often elliptic as they approach true leaves, even being abruptly narrowed at the base but not usually becoming more than 4 mm. in length. According to De Laubenfels, only in one group of *Dacrydium* do scale leaves follow juvenile leaves of his Type II, and, when scale leaves (Type III) are developed, they are never followed by any other leaf type. In sect. POLYPODIOPSIS, however, I find that all variations are exhibited in the alternation between scale leaves and foliage leaves. Main shoots may bear only scale leaves; a leafy branch which continues growth may first bear foliage leaves, then scale leaves. Leafy branches may have only one growth period with a dormant terminal bud or they may have at least one other burst of growth, as is evident in the leafy shoots where each growth period shows first an increase in leaf length to about the middle of the growth period, after which it again uniformly decreases; one to several pairs of scale leaves may separate the growth periods. The smallest of the leaves may be very similar to scale leaves and a pair of scale leaves is usually present in *P. comptonii* and *P. minor* at the first node of a leafy branch. Scale leaves have been found only on the special reproductive branchlets of *P. rospigliosii*.

The leaf anatomy, as seen in transverse sections of the foliage leaves, was described by Orr (22) for *Podocarpus vitiensis*, *P. minor*, and *P. rospigliosii*. The leaves are amphistomatic, and palisade parenchyma may be found on both sides or developed only on the side facing the light. The single vascular bundle is flanked by wings of transfusion tissue which sometimes extend fully half-way to the margin of the leaf. The extent of the transfusion tissue varies too much from one leaf to another for it to be used as a diagnostic character, but it is greatest in *P. minor* and *P. comptonii*. There is no organized accessory transfusion tissue, and isolated lignified cells with large lumina were detected only very rarely in the mesophyll, with none at all present in *P. rospigliosii*. I agree with Orr that *P. rospigliosii* has the greatest number of hypodermal fibers with often a continuous layer at the margin and midrib. In *P. vitiensis* and

P. filicifolius the hypodermal fibers are few, small, and often isolated even at the margin and midrib. In *P. minor* and *P. comptonii* the hypodermal fibers are larger and scattered, or grouped together, with the fewest in *P. minor*, except for an almost continuous layer at the margin. Vascular fibers are usually large and abundant above the midrib in all the species but are absent or rare below the midrib in *P. vitiensis*, *P. filicifolius*, and *P. rospigliosii*. The leaves of these latter species are thin, usually only between 0.3–0.6 mm. thick, those of *P. comptonii* are a little thicker (especially on fruiting branches), being from 0.5–0.8 mm., while *P. minor* has very thick leaves, from 0.6–1.2 mm.

The female strobili are remarkably similar in sections POLYPODIOPSIS, NAGEIA, and AFROCARPUS, even to the fertile bract adhering after the seed is separated from the axis at maturity. The detailed description of the ovule development of *Podocarpus vitiensis* by Gibbs (16) indicates a peduncle covered with imbricate scale leaves, succeeded by 6–10 bracts on the strobilus, the terminal one or two fertile. The portion of the peduncle covered by bracts might be designated as a woody receptacle, the uppermost 2–4 bracts subtending the ovule sometimes having definitely thickened adhering bases. This was not apparent to Gibbs in *P. vitiensis*, but that three sterile and one fertile bract unite to form a receptacle has been recognized in *P. minor* and *P. comptonii*. A thickened woody receptacle is very apparent on the mature seeds of *P. filicifolius*, where an additional pair of bracts may become involved.

In her observations on the wood structure of *Podocarpus*, Kaeiser (19) found that of species in sect. POLYPODIOPSIS usually like that of those in sections AFROCARPUS and NAGEIA.

In sect. POLYPODIOPSIS, Hair & Beuzenberg (18) counted the chromosomes of *P. vitiensis*, *P. comptonii*, and *P. minor* and found the $2n$ number to be 20. If one considers ten to be the basic number, this count affirms the suggestion that this section and sect. NAGEIA, in which $2n = 20$ in *P. blumei*, are the oldest groups in the genus.

KEY TO SPECIES OF SECT. POLYPODIOPSIS

A. All foliage leaves arranged pinnately on the twigs.
  B. Mature seed crested. ..... *P. rospigliosii.*[1]
  B. Mature seed not crested.
    C. Mature seeds pear shaped. ..... 1. *P. vitiensis.*
    C. Mature seeds spherical. ..... 2. *P. filicifolius.*

A. Some twigs pinnately leaved, but fertile twigs not flattened, and always bearing decussate foliage.
  D. Large trees; foliage mostly flattened; twigs pinnately leaved. ..... 3. *P. comptonii.*
  D. Small trees or shrubs; foliage mostly decussate; twigs rarely flattened. ..... 4. *P. minor.*

[1] This species treated previously in Jour. Arnold Arb. **29:** 118–122. 1948.

1. **Podocarpus vitiensis** Seemann, Bonplandia 10: 366. 1862, Jour. Bot. 1: 33. 1863, Fl. Vitiensis 266. 1865–73; Van Tieghem, Bull. Soc. Bot. Fr. 38: 169. 1891; Pilger, Pflanzenr. IV. 5(Heft 18): 63. 1903, Nat. Pflanzenfam. ed. 2. 13: 245. 1926; Gibbs, Jour. Linn. Soc. Bot. 39: 182. 1909, Ann. Bot. 26: 533. 1912; Stiles, Ann. Bot. 26: 455. 1912; Dallimore & Jackson, Handb. Conif. 58. 1923, 1931, 85. 1948; Florin, Sv. Vet-akad. Handl. III. 10: 275. 1931; Wasscher, Blumea 3: 425. 1941.

A large forest tree up to 43 m. high with trunk often over 1 m. in diameter (sometimes buttressed in New Guinea) and a crown of spreading branches. Young twigs decussate, usually in pairs at distances of 2.5–4 cm., spreading or erect-spreading, dimorphic; main twigs terete or slightly flattened below the ramifications, leafless, alternately bearing axillary decussate lateral leafy twigs and decussate, ovate to orbicular, deciduous bracts nearly 2 mm. long; lateral leafy twigs slender, usually unbranched, with the leaves usually smaller toward each end, decussate but turned in one plane, pinnately arranged, divaricate, the twigs up to 38 cm. long and terminated by small buds which may not develop. Terminal buds of main twigs globose or ovate, with decussate, ovate, orbicular, or obovate, obtuse scales, 1.5–2 mm. long. Leaves spread out in one plane by twisting at the base so that the adaxial sides are exposed on one side of the twigs and the abaxial sides exposed on the opposite side; leaf pairs 5–8 mm. apart; leaves sessile, lanceolate, rounded at the base and broadly decurrent, gradually narrowing toward the narrowly obtuse apices, amphistomatic, 1.5–3 cm. long by 3–5.5 mm. broad; midrib sometimes prominent on either surface and with stomata in the epidermis above and below. Leaves in transverse section with scattered hypodermal fibers on both sides, palisade mesophyll on upper, lower, or both sides, depending on the orientation of the leaf; a single median vascular bundle with a single resin canal (never 3) abaxial to the phloem and flanked by wings of transfusion tissue; vascular fibers conspicuous above the vascular bundle and no accessory transfusion tissue. Male strobili solitary or clustered 2 or 3, terminal on axillary leafy twigs or bracted pedicels, or on bracted main shoots often branching once or twice so that strobili or fertile branches may arise in bract or leaf axils, strobilus cylindrical, 12–20 mm. long and 2–2.5 mm. in diameter; microsporophylls triangular, with acute or obtuse tips, margins scarious. Female strobili terminal on peduncles in axils of bracts or normal leaves; peduncles 2–8 mm. long, sometimes branched, covered with 6–10 pairs of imbricate scale leaves; strobilus of 6–10 bracts, 1 or 2 fertile; receptacle not differentiated. Seed bluish red when ripe, to 2 cm. long, obliquely attached to receptacle, obovate, narrowed towards the base which may still bear the attached bract when the seed has fallen, apex obtuse; hard-coated inner seed terminated at the micropylar end by a sharp, sometimes recurved point.

DISTRIBUTION: In dense mixed forest, Fiji Islands, at altitudes between 100 and 900 m.; New Guinea, in the western part at altitudes of 1100–1200

m. and in the southeastern part at 1650–2000 m.; and Vanikoru, Solomon Islands.

Fiji Islands. VITI LEVU: Mba, Nandarivatu, *Degener 14483* (BISH, K, NY, US),[2] *14485* (MO), *14496* (A, NY), *Mead*, Sing. Field No. 1974 (K), *Parks 20653* (BISH, †UC), *Gibbs 674* (BM, K); valley of Singatoka River, *Gillespie 3273.2* (BISH), *3712* (BISH, DS, †UC), *3865* (BISH, K, NY, UC, US), *4308.1*, *4402.2* (BISH); Tailevu, e. of Wainimbuka River, *Smith 7076* (US). VANUA LEVU: Thakaundrove, Yanawei River, Mt. Kasi, *Smith 1796* (BISH, GH, NY, †UC, US). WITHOUT LOCALITY: *Horne 531* (GH, K), *Seemann 576* (Holotype, K; GH), *Graff* (K). **New Guinea.** NETHERLANDS NEW GUINEA: Idenburg River, Bernard Camp, *Brass 19534* (†A), *12787* (†A), *12787a* (A); Cyclops Mts., *Versteegh BW913* (LAE, †L); PAPUA: Alola, *Carr 14160* (A, †NY); Lala River, *Carr 15666* (†A, BM). **Solomon Islands.** Santa Cruz Group, Vanikoru, near Lemon River, *Walker B.S.I.P.212* (†A). **Cultivated.** AUSTRALIA: Bot. Gard. Sydney, *Boorman*, in 1908 (A), *Eames*, in 1937 (CU).

Even though *Podocarpus vitiensis* has been recognized as a species since 1862, an understanding of its relationships within the genus is quite recent. On the basis of the single vascular bundle in the leaf, stomata on both sides of the leaves, and supposedly two lateral resin canals as well as the one below the vascular bundle, Bertrand (1) put this species in a separate section, POLYPODIOPSIS. The confusion brought about by Bertrand and Mahlert (21) in ascribing the three vascular resin canals has been discussed previously (17) and referred to *P. rospigliosii* from South America which is now included in the same section.

Subsequently, Pilger (23) put *Podocarpus vitiensis* in his sect. NAGEIA on the basis of the opposite leaves which show the same characteristic turning of the leaf bases so that the lower surface is uppermost on one side of the twig and the upper surface on the other side of the twig when these decussate leaves orient themselves in the pinnate "fronds." Pilger's classification was followed by Gibbs (16) and Stiles (31) after Gibbs (15) had briefly considered sect. STACHYCARPUS. Florin (8) recognized the validity of Bertrand's sect. POLYPODIOPSIS for *P. vitiensis* as a separate group and added *P. minor*. This section is now well established.

All of these studies, including Gibbs' (16) description of the female

[2] The following symbols indicate the location of the specimens cited: Arnold Arboretum, Cambridge (A); Bernice P. Bishop Museum, Honolulu (BISH); Botanic Museum and Herbarium, Brisbane (BRI); British Museum (Natural History), London (BM); Jardin Botanique de l'Etat, Bruxelles (BR); Herbarium of the University of California, Berkeley (UC); Wiegand Herbarium, Cornell University, Ithaca (CU); Dudley Herbarium, Stanford University, Stanford (DS); Herbarium of the University of Georgia, Athens (GA); Gray Herbarium, Cambridge (GH); University of Illinois, Urbana (ILL); Herbarium and Library, Royal Botanic Gardens, Kew (K); Rijksherbarium, Leiden (L); Missouri Botanical Garden, Saint Louis (MO); Department of Forests, Papua and New Guinea, Lae (LAE); New York Botanical Garden, New York (NY); Muséum National d'Histoire Naturelle, Paris (P); United States National Museum, Washington (US); National Herbarium of Melbourne, Melbourne (MEL).

A dagger (†) preceding the abbreviation of an herbarium signifies that the details of the leaves of this specimen have been examined in transverse section.

strobilus, were on Fijian specimens of *Podocarpus vitiensis*. In 1944, Wasscher (32) recognized specimens of this species from New Guinea and, for the first time, described the dimorphic foliage which had been overlooked in the Fiji material. It is interesting that the early specimens (*Seemann 576*, *Graff s.n.*, and *Gibbs 674*) all have only terminal male cones on leafy twigs, whereas recent male specimens (*Degener 14496*, *Parks 20653*, *Smith 7076*) definitely show the dimorphic foliage, main twigs with scale leaves, and lateral leafy branches bearing male strobili or fertile branches bearing scale leaves and strobili or axillary branches bearing strobili.

New Guinea specimens may still prove to represent a separate species, but the half-matured ovules which I have seen are still pear-shaped and obliquely attached to the receptacle, as in the Fijian *Podocarpus vitiensis*.

Both Seemann (25) and Gibbs (16) have waxed eloquent on the beauties of this species and I must quote from Seemann: "This is one of the finest Coniferae I have ever seen. . . It attains sixty feet in height, has a stem nine feet in circumference, and has drooping, extremely graceful branches, which would render the species a highly desirable acquisition to our living collections."

2. Podocarpus filicifolius, sp. nov.

Arbor 15 m. alta ramulis numerosis, divaricatis, spiralibus vel oppositis; alabastris in ramulis principalibus parvis, late ovatis, squamis paucis, late triangularibus decussatis, 1.5–2 mm. longis; alabastris in ramulis foliiferis permutatis, ovatis, plerumque constanter dormientibus; foliis dimorphis; squamis in ramulis principalibus, divaricatis, tenuibus; late triangularibus, 2 mm. longis, acutis vel obtusis; foliis ad ramulis pinnatis terminalibus vel axillaribus, sessilibus, divaricatis, oppositis, 6–24 mm. longis, 3.5–4.5 mm. latis, lanceolatis, tenuibus, planis, apice late acutis, basi late rotundatis, decurrentibus, costa non manifesta; strobilis masculis ignotis; strobilis femineis solitariis (?), pedunculis 10 mm. longis, squamas 4–6 binas decussatas vel cicatrices gerentibus; receptaculo parvo lignoso bracteis oppositis 2 late obtusis subtento, 7 mm. longo, 3 mm. lato, bracteis 3 coalescentibus equalibus, apice liberis composito, bractea unica fertili; semine maturo globoso, 1.5–1.8 cm. longo et lato, apice aequaliter rotundo, obtuso.

DISTRIBUTION: Morotai, in the Moluccas.

Moluccas. Morotai, *A. Kostermans*, in 1949 (Holotype, †L).

This tree differs from *Podocarpus vitiensis* in the spreading scale leaves, thinner foliage leaves, the distinct receptacle 7 mm. long supporting the seeds, and the spherical seeds. The dissected seed shows a smooth, brown outer coat 0.3 mm. thick, a hard, woody, light tan middle layer which is pointed at the micropyle, and a thin papery brown inner layer.

The name refers to the fern-like appearance of the pinnately leaved twigs, reminiscent of the royal fern, *Osmunda regalis*.

3. **Podocarpus comptonii** Buchholz, Bull. Mus. Hist. Nat. Paris II. 21: 284. 1949; Guillaumin, Acta Horti Gothob. 19: 8. 1952; Chevalier, Études Mélanésiennes II. 1: 114. 1956.

A tree becoming 10–12 m. high with trunk up to 80 cm. or more in diameter, bearing few branches below but profusely branched above; bark brownish, longitudinally furrowed; young twigs green and showing decurrent leaf bases; branches erect or ascending, usually opposite while still young; terminal buds appearing naked but protected by special scales which become part of foliage but do not grow into leaves. Foliage dimorphic; scale leaves on main twigs decussate, broadly triangular, decurrent, 2 mm. long, becoming obtuse, then ovate-elliptic, divaricate, 3–4 mm. long; 1 pair opposite scale leaves usually at first node of leafy twigs; leaves decussate, emerging in 4 ranks from the twigs and, on vigorous branches, twisted at the base so that the pinnately leaved twigs bear opposite leaves, on one side all with the abaxial side exposed and on the other side the adaxial; on upper reproductive branches of mature trees, leaves held obliquely in 4 vertical ranks; leaves lanceolate to elliptic, obtuse, 7–15 mm. long, 2–5 mm. wide, thick, sessile, with decurrent leaf bases; single midrib not usually distinct, with the surface becoming dry in many longitudinal wrinkles. Usually only foliage leaves on small vigorous plants and seedlings becoming 30 mm. long, 6 mm. wide, very thin, acutish, and opposite on pinnate twigs. Leaves differentially amphistomatic, varying with the orientation; transverse sections showing hypoderm interrupted by the stomatal rows, single vascular bundle with single resin canal below phloem, transfusion tissue well developed, no accessory transfusion tissue, vascular sclereids abundant above the bundle with fewer below; palisade mesophyll on either or both sides depending on leaf orientation. Male strobili sessile and terminal on lateral twigs usually bearing regular foliage leaves, subtended by a pair of narrow, short foliage leaves or bracts; strobili ovoid, 5–6 mm. long, 3 mm. wide; microsporophylls broadly triangular, apices acute, margins thin and somewhat erose. Female strobili terminal on lateral twigs which may bear ordinary foliage leaves or spreading scale leaves; each strobilus bearing 3 or 4 pairs of small, opposite, sterile bracts on an axis 10 mm. or more long, with the two upper bracts unequal and forming a nonfleshy receptacle, one of the bracts fertile. Seed obovoid, 25 mm. long, 18–20 mm. diameter, fleshy, red (?) when ripe; kernel with two ridges to a straight or curved beak at the micropyle.

DISTRIBUTION: In forests on mountain slopes of New Caledonia above 1000 m. altitude.

New Caledonia. Mt. Ignambi, *Compton 1524* (†BM), *1587* (†BM); Mt. Mou, *Vieillard 1275* (†P), *3064* (†GH), *3264* (†P), *Buchholz 1085* (†ILL), *1421*, *1452*, *1474*, *1578* (ILL), *1684* (Holotype, †ILL), *1697* (ILL), *MacDaniels 2323* (CU), *Virot* in 1938 (A), *White 2033* (†A, BRI), *De Laubenfels P129* (GA), *Compton 607* (BM); Mt. Humboldt, *Schlechter 15331* (†BR, †BM), Mt. Dzumac, *De Laubenfels 153* (GA), Montagne des Sources, *De Laubenfels 123* (GA); Koe,

Balansa 184 (†P); Plain des Lacs, Mons du Mai Forest, *Buchholz 1350, 1350a, 1697* (ILL); Bai des Piroques, *White 2120* (†A, 2 sheets); beside River Blanche, *Ingle I.66* (†MEL); River Tane & Bourail, *Balansa 1385* (K). No specified locality, *Buchholz 1539a* (†MO).

The twig dimorphism observed and described by Wasscher (32) for *Podocarpus vitiensis* is likewise very apparent in *P. comptonii.* The plant bears several kinds of foliage: definitely acute triangular scale leaves on vigorously growing main shoots; ovate or elliptic scale leaves on main shoots and lower parts of twigs; true foliage leaves lanceolate and arranged pinnately; and elliptic foliage leaves arranged on the twigs decussately. Variations, such as twigs bearing alternately scale leaves and foliage leaves for three growth periods with no branching, or branches bearing foliage leaves becoming main branches but subsequently bearing only scale leaves of either kind, are numerous.

This species has long been confused with *Podocarpus minor* which is a small tree along streams and in swamps at lower elevations. Compton (5), who strangely saw only the large trees, remarked on the inappropriateness of the name "*minor.*" All the specimens he assigned to *P. minor* belong here. The specimen *White 2120* from the Arnold Arboretum was labeled *P. vitiensis*, showing that it was recognized as being different from *P. minor.* Dr. J. T. Buchholz collected both species abundantly and the differences became clear to him. The specimen *Compton 1273*, listed as an undetermined species, belongs here.

4. **Podocarpus minor** (Carrière) Parlatore in DC. Prodr. **16**(*2*): 509. 1868; Brongn. & Gris, Bull. Soc. Bot. Fr. **16**: 326. 1869; Mahlert, Bot. Centralbl. **24**: 281. 1885; Pilger, Pflanzenr. IV. **5**(Heft 18): 62. 1903, Nat. Pflanzenfam. ed. 2. **13**: 245. 1926; Schlechter, Bot. Jahrb. **38**: 16. 1907; Compton, Jour. Linn. Soc. Bot. **45**: 425. 1922; Dallimore & Jackson, Handb. Conif. 51. 1923, 1931, 75. 1948; White, Wilson & Guillaumin, Jour. Arnold Arb. **7**: 78. 1926; Florin, Sv. Vet-akad. Handl. III. **10**: 278. 1931; Guillaumin, Acta Horti Gothob. **19**: 8. 1952; Chevalier, Études Mélanésiennes II. **1**: 114. 1957.

Nageia minor Carrière, Traité Gén. Conifères. ed. 2. 641. 1867.
Podocarpus palustris Buchholz, Bull. Mus. Hist. Nat. Paris II. **21**: 284. 1949; Chevalier, Études Mélanésiennes II. **1**: 114. 1957.

A dwarf tree or shrub, 2–3 m. high, trunk 15–30 cm. in diameter with numerous ascending branches; bark rough, brown or dark gray; twigs opposite on young stems or scattered, ridged by decurrent leaf bases; terminal buds normally small with few opposite scales, frequently abnormally enlarged due to infestation by insect larvae. Leaves dimorphic; scale leaves on main shoots often deciduous, decussate, triangular-obtuse, keeled, decurrent, 1 mm. long, becoming divaricate, elliptic, thick, to 4 mm. long, and usually 1 pair of elliptic scale leaves at the first node of leafy branches; foliage leaves crowded on short branchlets, opposite, de-

cussate, ascending and held obliquely in 4 vertical ranks, oval or elliptic, obtuse, sessile, 10–20 mm. long. 3.5–5.5 mm. wide, thick and longitudinally wrinkled when dry, with broadly decurrent bases; midrib not evident. Leaves differentially amphistomatic with twice as many stomata on the adaxial side, stomata easily seen under low magnification on young leaves as minute white dots. Transverse sections of leaves showing rare hypodermal fibers on both sides but abundant at the margins, palisade mesophyll on both sides, a broad midvein due to extension of transfusion tissue half-way to the margin, single resin canal, usually abundant vascular sclereids above and below the vascular bundle. Male strobili terminal on short, bracted peduncles, 1–1.5 mm. long, in clusters of 3–5 or more at ends of short lateral leafy twigs; 5–8 mm. long, 2.5–3 mm. in diameter; microsporophylls broadly hastate with narrowly acute upturned apiculi. Female strobili terminal on lateral twigs, axis 4 mm. long; strobili of 3 or 4 pairs of decussate bracts 1–2 mm. long; immature ovules usually crested, long-pyriform; 1 terminal fertile bract (rarely 2), keeled, 2 mm. long and spread upon the back of the base of the large seed (away from the micropyle) with minute or suppressed apex, the 2 upper bracts fusing into a small receptacle 4 mm. long. Seed crested, obliquely conically pyriform, 2.8 cm. long, 1.7 cm. wide, becoming maroon-red when ripe; inner woody layer usually obtuse, with a beak formed at the micropyle, usually straight.

DISTRIBUTION: Along banks of streams and lakes on Plaine des Lacs and near Prony Bay, New Caledonia.

New Caledonia. Borders of Lac Arnaud, *Vieillard 1275* (Holotype of *P. minor*, †P; BM, †NOUMEA), *Vieillard* or *Deplanche 170* (†P); Plaine des Lacs, River des Lacs, *Buchholz 1719* (†ILL), *1729* (†ILL), *LeRat 607* (†BM), 22 km. Station, *Buchholz 1347* (†ILL), *1348* (ILL), *1421* (Holotype of *P. palustris*, †ILL; P), flooded lake shore, headwaters of Yate R., *De Laubenfels P112* (GA), Rio des Pirogues, *White 2261* (BRI, †UC, US); Lac en Huit, *De Laubenfels P115* (GA), *McKee 3382* (US); river sw. of Grand Lac, *Virot 658* (†A), *MacDaniels 2544* (†CU); Prony, *Frank 207 Ser. A* (†BM, BRI, †F, †UC, US); Baie du Sud, *Vieillard 1275* (A, BM). Without specific locality: *Levormand 9171* (†K), *Raoul s.n.* (†P), *Petit N138* (†P), *LeRat 1752* (†P).

At some sites these dwarf trees grow very slowly and become very old, their bases often growing in standing water and becoming buttressed. At times they may be entirely submerged beneath muddy, silt-laden water, reddish from the ferruginous soil carried down from the surrounding mountains during heavy rains. Dr. Buchholz (*ms.* data) believed there to be a related species, *Podocarpus palustris* which he described, but the differences he listed do not fall outside the normal range of variation in *P. minor*, and the difference in wood density is no more than expected from the slightly different ecological habitats.

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